

Selective influences on the coastal plateau of Mendocino County have sorted out a combination of species with unique qualities for survival in one of the most extreme soil situations in California. The pygmy forests which have resulted from this selective action include much of the natural distribution of both *Cupressus pygmaea* and *Pinus bolanderi*. The gigantic *Sequoia-Pseudotsuga* forests which grow in adjacent portions of the coastal plateau present an amazing contrast in vegetational selection.

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AN INTERSPECIFIC CROSS IN CUCURBITA (*C. LUNDELLIANA* BAILEY \times *C. MOSCHATA* DUCH.)

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As one aspect of a comprehensive study of the origin and relationship of the cultivated species of *Cucurbita*, *C. lundelliana* Bailey, a non-cultivated species, was crossed with *C. moschata* Duch., one of the five cultivated species of the genus. In *Cucurbita* successful crosses between truly wild species and domesticated ones have not been hitherto reported. Essentially the cross *C. lundelliana* \times *C. moschata* combines two genotypes, the one (*C. lundelliana*) a wild species and the other (*C. moschata*) with a long history of cultivation. The hybridization experiments reported here were made with the idea that the compatibility relations might indicate directions in which to search for the common ancestor of the cultivated group, and perhaps suggest in a general way the area where the cultivated forms were domesticated (Whitaker, 1956). Furthermore, it was thought that the results would contribute to an understanding of the heritability of characters such as large fruit, large seed, soft rind, etc., which have value under cultivation. The results reported here provide partial answers to some of these questions.

MATERIALS AND METHODS

Cucurbita lundelliana, the Peten gourd, is endemic in Central America. It has been collected in Guatemala, British Honduras, and southern Mexico (Yucatan). The plants are strong, vigorous annuals, with fine,

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wiry stems and deeply lobed leaves having a greyish-green cast (fig. 1B). The flowers of both sexes are large, showy and upright (fig. 1E). The fruits are almost round, dark green, often striped, and have hard rinds, or shells (fig. 2A). The flesh is greenish white and the placenta is solid. The seeds are comparatively small and numerous and have characteristic broad, wavy margins.

Cucurbita moschata cv. Long Genoa Queen is an old and little-known cultivar quite typical of the species. The modern cultivar Butternut of *C. moschata* probably originated as a selection from Long Genoa Queen. The plants have good vigor, large, ovoid leaves, slightly triangular lobed (fig. 1A); long fruits (19 to 36 inches), with an enlarged terminal portion that contains the seeds (fig. 2B). The flesh is dark-orange, moist and slightly stringy.

Both *C. lundelliana* and *C. moschata* have 20 pairs of chromosomes. Unfortunately, it has not been possible to study cytologically the progenies of the cross between them.

Matings of *C. lundelliana* and *C. moschata* cv. Long Genoa Queen produced fruits with numerous fertile seeds. The F_1 proved to be self-fertile and cross-fertile with each parent. In the summer of 1954, the parents and the F_1 were grown in the experimental garden along with several F_2 and backcross progenies. The analysis of the data obtained from the measurements and observations of these progenies constitutes the basis for this report.

Measurements were made of leaf blade length and width, lobe depth and petiole diameter. For male and female flowers the following measurements were obtained: length of corolla, corolla limb, sepal, style plus stigma, staminal column, and ovary length and diameter. Other measurements included fruit length and diameter and length and diameter of several typical seeds. Fruit color, rind hardness, fruit construction, flesh color, and placenta type were also recorded.

The large sprawling plants of most species of *Cucurbita* require extensive space to mature. For this reason it is impractical to raise by conventional methods the number of plants required for a convincing genetical analysis. A more practical method of analysis adapted to the data obtained from this study was suggested by Anderson (1949, 1954), and is the method used herein. Using this method several key characters are chosen for measurement and study, exercising care to select those characters that best represent the differences between the species. Frequency distributions of the scores of each character will indicate in graphical fashion whether the two species overlap in a particular character. More effective in demonstrating the pattern of variation between species is the hybrid index which can be computed from these data. It is designed to show variation of several characters simultaneously. Such an analysis has the advantage of sharply displaying the pattern of differences and resemblances between species, and at the same time suggests how some of the characters that differentiate species are inherited. Stebbins and Ferlan (1956) used this

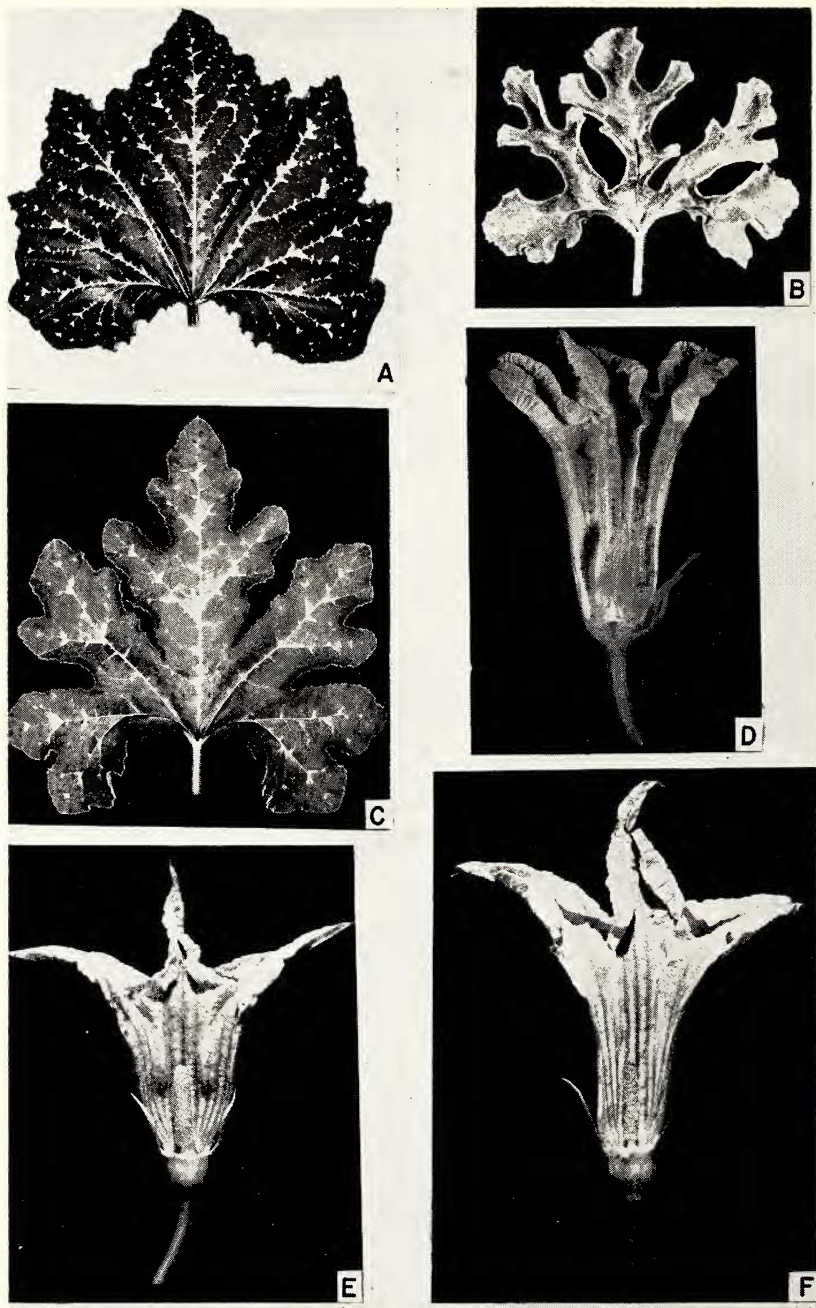


FIG. 1. Leaves and flowers of *C. lundelliana*, *C. moschata*, and F_1 hybrid.

method for investigating the role of hybridization in the origin of intra-specific polymorphism in *Ophrys*, where direct genetic experiments are not feasible for various reasons.

RESULTS

DESCRIPTION OF CHARACTERS USED IN DEVELOPING THE HYBRID INDEX.

To treat the measurement and observational data in an objective manner, seven characters were arbitrarily selected for analysis. A hybrid index was computed from data similar to those recorded in Table 1 for the parents. In calculating the values for the hybrid index equal weight was arbitrarily assigned to each character. The character expressions are described as follows.

1. Leaf length / lobe depth. In *C. lundelliana* the leaves are deeply lobed (fig. 1B) as contrasted with the shallow-lobed leaves of *C. moschata* (fig. 1A). This difference is reflected in proportionately larger ratios as the leaf approaches the unlobed condition. The ratios for *C. lundelliana* range from 1.92 to 2.67; those for *C. moschata* from 5.00 to 10.60; and those for the F_1 from 3.00 to 9.00.

2. Leaf width. The leaves of *C. lundelliana* are generally much narrower than those of *C. moschata*. Leaves of *C. lundelliana* range in width from 11.5 to 15.0 cm; those of *C. moschata* from 15.5 to 31.5 cm; and those of the F_1 from 13.0 to 20.5 cm.

3. Petiole. The petioles of *C. lundelliana* are slender and reed-like, while those of *C. moschata* are stouter and more rigid. A measure of this difference is the diameter of the petiole at the point of attachment to the stem. Petiole diameter in *C. lundelliana* ranges from 0.2 to 0.4 cm; in *C. moschata* from 0.7 to 1.0 cm; in the F_1 from 0.4 to 0.6 cm.

4. Length ♂ corolla / length ♀ corolla. In *C. lundelliana* the corollas of the pistillate flowers are usually somewhat longer than those of comparable staminate flowers on the same plant, while in *C. moschata* the corollas of the pistillate and staminate flowers are about equal in length. The ratios for *C. lundelliana* range from 0.41 to 0.80; for *C. moschata* from 0.84 to 1.45; and for the F_1 hybrid from 0.57 to 1.00.

5. Fruit length / fruit width. The fruit of *C. lundelliana* is short and ellipsoidal to almost round (fig. 2A), while that of *C. moschata* is long, slender, with an enlarged terminal portion containing the seed cavity (fig. 2B). Fruits of the F_1 are phenotypically very different from those of the parents and have a constricted neck portion (fig. 2C).

FIG. 1. Leaves and flowers of *C. lundelliana*, *C. moschata*, and F_1 hybrid. A, leaf of *C. moschata* with shallow lobes and stout petiole; B, leaf of *C. lundelliana* with deep finger-like lobes and slender petiole with long hairs; C, leaf of F_1 , which appears to be about intermediate between the two species; D, staminate flower of *C. moschata*, which has short, broad corolla lobes, broad flat sepals, and a stout pedicel; E, staminate flower of *C. lundelliana*, with long, pointed corolla lobes, slender, thread-like sepals, and goblet-shaped calyx tube with slender pedicel; F, staminate flower of F_1 , which has the long, lobed corolla, slender sepals and the goblet-shaped calyx of *C. lundelliana* but has a relatively stout pedicel, $\times 0.48$.

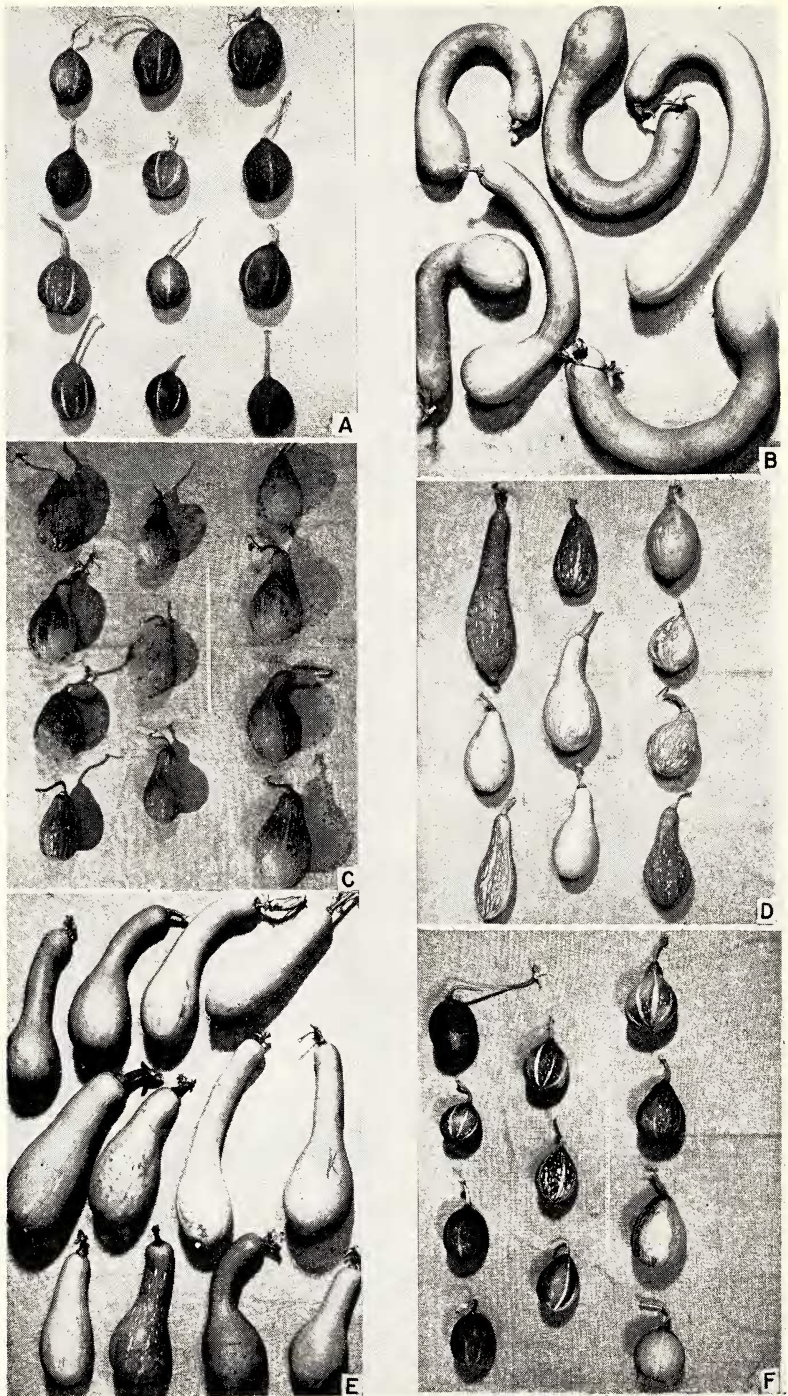


FIG. 2. Fruits of parents and progenies of *C. lundelliana* X *C. moschata*. A, *C. lundelliana*; B, *C. moschata*; C, F₁; D, F₂; E, F₁ backcrossed to *C. moschata*; F, F₁ backcrossed to *C. lundelliana*.

TABLE 1. DATA USED IN COMPUTING AND CONSTRUCTING THE HYBRID INDEX FROM SIX CHARACTERS FOR *C. LUNDELLIANA* AND *C. MOSCHATA**

Species and plant no.	Leaf length Lobe depth	Leaf width (cm)	Petiole diameter (cm)	Length ♂ Length ♀	corolla corolla	Fruit length Fruit width	Seed area (sq. cm)	Index value
<i>C. lundelliana</i>								
5-1	2.56	11.5	0.4	0.71		1.15	0.5	1
5-2	2.27	14.0	0.3	0.64		1.08	0.5	1
5-3	2.17	13.5	0.4	0.54		1.15	0.5	0
5-4	2.36	13.5	0.4	0.52		1.13	0.5	0
5-5	1.92	14.5	0.4	0.41		1.07	0.5	1
5-6	2.67	12.5	0.3	0.52		1.13	0.5	1
5-7	2.60	13.0	0.3	0.50		1.19	0.5	0
5-8	2.27	12.0	0.3	0.60		1.00	0.5	0
5-9	2.50	13.0	0.3	0.63		1.08	0.5	1
5-10	2.50	11.5	0.2	0.75		1.07	0.5	1
5-11	2.33	15.0	0.4	0.58		1.06	0.5	1
5-12	2.30	13.0	0.3	0.80		1.07	0.5	1
<i>C. moschata</i>								
24-1	6.43	15.5	0.8	1.11		4.96	2.0	13
24-2	7.40	21.0	0.7	0.96		6.35	2.0	14
24-3	6.75	30.5	1.0	1.09		7.72	2.0	14
24-4	6.43	25.5	0.7	0.86		4.79	2.0	13
24-5	5.38	25.0	0.8	0.84		4.58	2.0	13
24-6	6.43	24.5	0.7	0.91		5.71	2.0	14
24-7	7.67	26.0	0.8	0.88		6.83	2.0	13
24-8	7.00	23.0	0.7	1.04		5.14	2.0	14
24-9	5.78	31.5	1.0	1.00		7.36	2.0	14
24-10	5.00	25.0	0.8	1.45		6.92	2.0	13
24-11	10.60	30.0	0.8	1.00		5.63	1.5	13
24-12	10.20	28.0	0.7	1.31		5.96	2.0	14

* The seventh character used in computing the hybrid index is not included in the table, since all fruits of *C. lundelliana* have hard rinds and solid placenta, while those of *C. moschata* are non-hard and non-solid. In computing the hybrid index all characters were arbitrarily given equal weight. Each individual was assigned one of three scores for each of the 7 characters; 0=similar to *C. lundelliana*; 2=similar to *C. moschata*; 1=intermediate. Employing this scheme, "pure" *C. lundelliana* =0, while "pure" *C. moschata* =14.

6. Hardness of rind and type of placenta. These two qualitative characters have been combined in the hybrid index. Fruits of *C. lundelliana* have hard, woody rinds that do not decay readily and cannot be cut with an ordinary knife. The seeds are embedded in the solid placenta (fig. 3A, right). *Cucurbita moschata* has a relatively soft rind that can be cut easily even at full maturity, while the placenta is loose and stringy and collapses at maturity leaving a large cavity (fig. 3A, left). The F₁ hybrid (fig. 3A, center) has a hard rind and a more or less open placenta.

7. Seed area. *Cucurbita lundelliana* has relatively small seeds with an area of about 0.5 sq. cm. for each seed (fig. 3B, bottom); *C. moschata* has much larger seeds with an area of about 2.0 sq. cm. per seed (fig. 3B, top). Seeds of the F₁ are about intermediate in area; they range from 0.65 to 1.35 sq. cm. (fig. 3B, center).

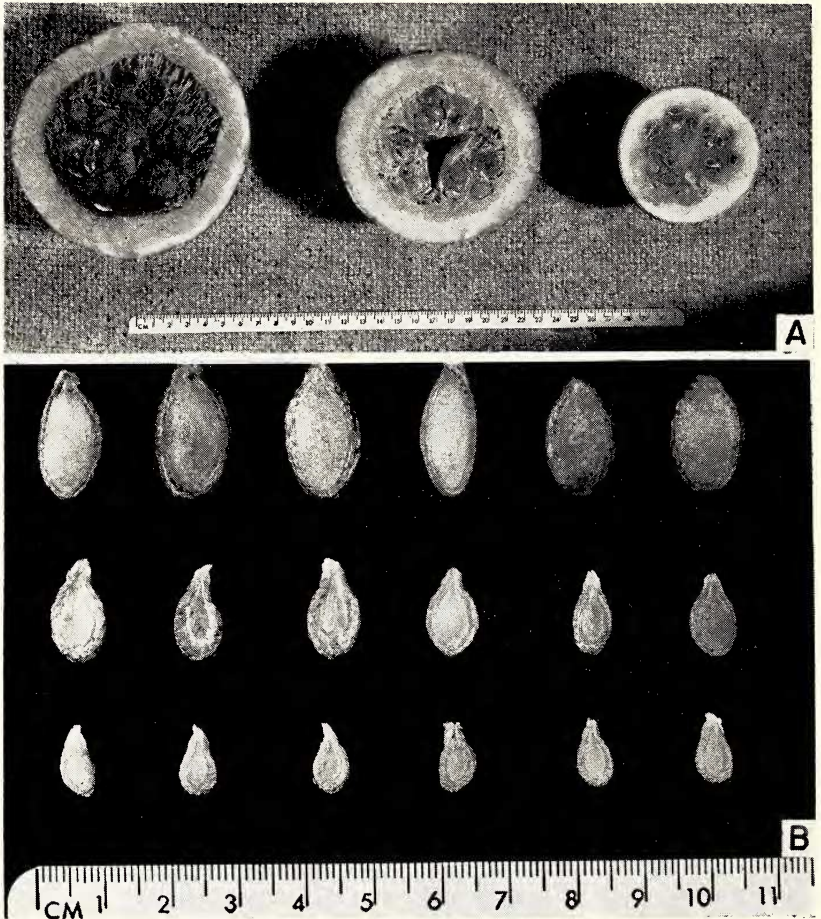


FIG. 3. A, cross sections of fruits of *C. moschata* (left), F_1 hybrid (center), *C. lundelliana* (right); B, seeds of *C. moschata* (top), F_1 hybrid (center), *C. lundelliana* (bottom).

DESCRIPTION OF THE F_1 . The F_1 plants were vigorous and thrifty and had foliage somewhat darker green than either parent. An occasional plant in the F_1 progenies had abnormal leaves and stems. Such plants died before producing flowers or maturing fruits. Of the total population of 28 F_1 plants, 7 were male-sterile. The male-sterile plants produced neither abortive nor male flowers. The F_1 plants were approximately intermediate between those of the two species in most characters (see figs. 1 and 2). The frequency distribution of hybrid index values (fig. 4) indicates a minimum overlapping of the F_1 into either species in the characters selected for analysis. There was a wide variation in pollen fertility ranging from 17 to 74%, with a mean of 42% for the 17 plants sampled.

TABLE 2. FERTILITY OF PARENTS, F₁, F₂, and BACKCROSSES OF CUCURBITA
LUNDELLIANA X C. MOSCHATA

Parent or progeny	Total plants (number)	♀ -Sterile plants (number)	♂ -Sterile plants (number)	Pollen fertility	
				Mean (percent)	Range (percent)
<i>C. lundelliana</i>	12	0	0	96	85-99
<i>C. moschata</i>	12	0	0	93	80-99
F ₁	28	0	7	42	17-74
F ₂	27	1	8	39	10-74
Backcross to <i>C. lundelliana</i>	72	4	0	76	6-88
Backcross to <i>C. moschata</i>	67	0	2?	48	9-94

DESCRIPTION OF THE F₂. The bulk of the F₂ segregates were more nearly comparable with *C. lundelliana* than with *C. moschata*. In fact, for most characters the F₂ scarcely exceeded the F₁ in the direction of *C. moschata* in our sample of 27 F₂ plants. This conclusion is substantiated by the histogram of the hybrid index values (fig. 4). The different sizes and shapes of fruit produced by the segregates are shown in figure 2D. There were 8 male-sterile plants in the population of 27 plants from 4 progenies. The F₂ segregates were characterized by a wide range in pollen fertility (10 to 74%; mean 39%).

DESCRIPTION OF BACKCROSSES. The most noticeable feature of the backcross progenies was their phenotypic similarity to the recurrent parent. In general this was true of vine, flower, and fruit characters. The photographs of the fruits (figs. 2E and 2F) illustrate this point very nicely. The frequency distributions of the hybrid index values (fig. 4) suggest that the population from the backcross to *C. moschata* is more variable than that from the backcross to *C. lundelliana*. Superficially the backcrosses looked as if they might have been slightly more variable populations of either parent.

FERTILITY OF PARENTS AND PROGENIES. For the purpose of this study it was important to know something about the fertility of the individuals comprising the F₁, F₂, and backcrosses. Table 2 summarizes the data obtained from field observations and pollen counts.

The data of Table 2 indicate that about one quarter of the F₁ and F₂ individuals from the cross are male-sterile. Plants which did not produce male flowers and those which produced male flowers but aborted prior to anthesis were lumped in this category. It is worth noting that there was not a single clear-cut case of male sterility in the backcross progenies. One plant in the F₂ and 4 plants in the backcross to *C. lundelliana* were males; that is, no female flowers were produced. The pollen fertility of the parent species is very nearly identical (mean 93 and 96%), while the means of the F₁ and F₂ are not very different (42 and 39%). On the other hand the mean pollen fertility for the backcross to *C. lundelliana* was 76% (range 6 to 88%) and that for the backcross to *C. moschata* was only 48% (range 9 to 94%). This sharp difference in mean fertility be-

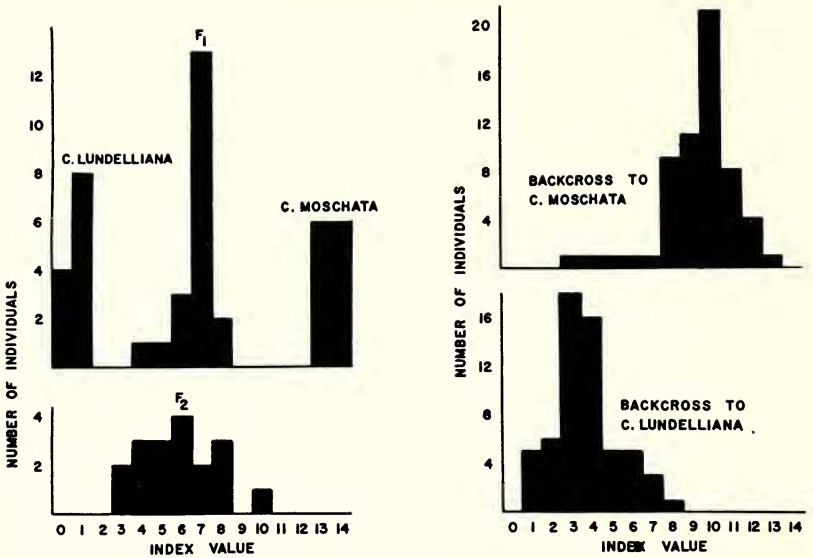


FIG. 4. Frequency distributions of hybrid index values for *Cucurbita lundelliana*, *C. moschata*, their F_1 , F_2 , and backcross progenies to both parent species (further explanation in the text).

tween the backcross progenies suggests that maternal or cytoplasmic factors are effective in restoring to a marked degree the pollen fertility of the progenies of the backcross to the maternal parent.

DISCUSSION

The method of analysis chosen for this study has many shortcomings, but it does illustrate certain characters by which the two species differ, and gives a rough quantitative measure of these differences.

The data suggest that some fruit characters, such as large size, soft rind, highly colored flesh, and large seeds, which presumably have value under cultivation, are for the most part recessive. On the other hand, vegetative and flower characters, which in this instance appear to be of less importance under domestication, are intermediate in their expression.

Although the backcross progenies are remarkably similar to the recurrent parent in fruit characters, the frequency distribution of the hybrid-index values (fig. 4) suggests that genes of the other parent are present. The subtle nature of this hereditary contribution cannot be detected except by careful study.

The frequency distribution of the hybrid-index values (fig. 4) indicates that while the F_2 values were considerably more variable than the F_1 , as would normally be anticipated, they did not reach values of either of the parent species in the population sampled. The backcross to *C. lundelliana* extends up to the modal class of *C. lundelliana*. However, its own mode is about halfway between the *C. lundelliana* mode and the F_1 mode.

The backcross to *C. moschata* barely reaches the mode of *C. moschata*, and again its mode is approximately halfway between those of the recurrent parent and the F_1 .

SUMMARY AND CONCLUSIONS

1. Controlled pollinations demonstrated that a wild annual species of *Cucurbita* (*C. lundelliana*) can exchange genes with a cultivated species (*C. moschata*). The F_1 is fertile enough to produce F_2 and backcross progenies. Individuals of these progenies are fertile in varying degrees except for some male sterility in the F_1 and F_2 generations and for one backcross progeny that had at least 4 individuals that were female-sterile.

2. The parent species are well separated by differences in important morphological characters. This separation is illustrated by frequency distributions constructed from hybrid-index values. From the frequency distributions it is evident that of the 7 characters selected for analysis none are overlapping. The F_1 is intermediate between the parents in the characters selected for analysis except for the qualitative characters—rind hardness and placenta type. An analysis shows that in most characters, the F_2 population barely exceeds the F_1 in the direction of *C. moschata*. This analysis combined with a similar analysis of the backcross progenies suggests that *C. moschata* has many recessive genes.

3. Comparisons of the backcross progenies indicate that they are strikingly similar to the recurrent parent in appearance. This finding suggests that various isolating barriers such as linkage, selective fertilization, and differential viability affect the backcross.

4. If compatibility relations are used as criteria, the isolating barriers that prevent crossing between *C. lundelliana* and *C. moschata* are not well developed in spite of the great morphological diversity between the species. There seems no doubt that each species is a good taxonomic entity. It is equally clear that the two species have a number of genes in common. For this reason it is not unreasonable to suggest that *C. moschata* may have been derived from *C. lundelliana* by isolation and subsequent selection by man. An alternative suggestion would be that both species were derived from a common ancestor, but when domesticated, *C. moschata* diverged sharply by natural selection under the guidance of man.

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